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## NOTES ON THE OCCURRENCE OF ABNORMAL MITOSES IN SPERMATOGENESIS.

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Mitotic figures abnormal particularly with respect to the number of chromosomes and centrioles involved are, as is well known, of common occurrence in the spermatogenesis of many insects. Apart from their interest as mere abnormalities, these cases sometimes throw light on more important problems of cell division and acquire, therefore, a much greater significance. In the course of several years' study of hemipteran (Family *Pentatomidæ*) spermatogenesis a variety of abnormal types of division have been observed, and it has seemed worth while to assemble descriptions of some of these, in particular those not hitherto described by other workers. The cases here reported are all from the male germ cells of various Hemiptera, belonging with one exception to the Family *Pentatomidæ*. The material was originally fixed for a variety of different purposes and the methods are accordingly noted separately where necessary. I am indebted to Professor E. B. Wilson for the use of a number of slides of *Loxa florida* which he had prepared some years ago and which I found presented a very unusual type of cell division.

Abnormal mitoses occur sometimes as solitary exceptions among many normal cells, but at other times they occur in large numbers in a single testis. In the latter case the abnormal cells may form a large percentage of the cells in a single spermatic cyst. Frequently the condition which produces these irregularities is more widely operative with the result that large numbers of cells in a given testicular lobe or follicle are involved. The isolated cases are doubtless due to occasional 'accidents' such as are to be expected in all vital phenomena; but the simultaneous occurrence of many abnormal divisions seems sometimes to depend on other causes, the nature of which is for the most part unknown.

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There are obviously three possible types of abnormal cell division, which may be outlined as follows:

*Case 1.*—The number of chromosomes is normal, but the number of centrioles is abnormal.

*Case 2.*—The number of centrioles is normal, but the number of chromosomes is abnormal.

*Case 3.*—The number of both chromosomes and centrioles is abnormal.

Examples of these three cases will be considered in order.

#### CASE 1.

The occurrence of dividing cells in which a normal number of chromosomes is arranged on a multipolar spindle is very rare. Indeed, I have found only a single case of this kind, and do not recall having noted any similar cases in the published work of other writers. This unusual example was found in a testis of *Chelinidea vittiger* Uhl. (Family *Coreidae*), which did not present any other unusual features. In the male of *Chelinidea* the spermatogonial chromosomes number twenty-one, of which two are very small—so-called *m* chromosomes—and one, an unpaired X chromosome. In the first maturation division the chromosomes, eleven in number, are arranged in the manner characteristic of other coreids.

The abnormal division here reported occurs in a cyst of spermatocytes in the metaphase of the first maturation division. The spindle is tri-polar (Fig. 3) and the centriole at each pole can be distinctly identified. The legs of the triangular spindle figure are nearly but not quite equal; otherwise it is very regular in formation. The eleven chromosomes characteristic of this division can be easily counted, and in most cases their distribution to the spindle poles can be foretold. Their arrangement on the spindle is very regular, and it will be readily seen that each pole of the spindle will receive approximately the same number of anaphase chromosomes. In the figure the chromosomes are numbered according to the approximate level of focus at which they appear, No. 1 being the topmost (the two topmost chromosomes (No. 1) were added from a contiguous section).

The disposition of the *m* chromosomes is particularly interest-

ing. Ordinarily they conjugate very briefly on the spindle (Wilson, '05*b*), and then separate precociously; but in this case they seem to have gone on the spindle entirely separate from each other (even their customary semblance of synapsis has failed). One gets the impression that they receive spindle fiber attachments at both ends, although a single one might be expected if such attachments are invariably specific.

The origin of the third centriole in a case of this kind is obscure, but it is possible that a tripolar spindle might arise through the precocious separation of one of the pairs into which the centrioles of the hemiptera are characteristically divided at an early stage in the growth period of the primary spermatocytes; but the staining of the centrioles in the case which I have described was not sufficiently precise to permit analysis of this possibility.

#### CASE 2.

Cases in which normal, bipolar spindles are developed in connection with an unusual number of chromosomes are of not infrequent occurrence. The best known examples are to be found in triploid and tetraploid "mutants," in which the abnormal chromosome number exists in all the cells of the body. Similar multiplications of the normal chromosomal complex likewise occur in the germ cells of normal individuals with some frequency, either as isolated cases or in groups. Henking ('91), who first made a critical examination of hemipteran chromosomes (in *Pyrrhocoris*), seems to have noted a case of the occurrence of the diploid chromosome number in the first maturation division (Henking ('91), Fig. 30*a*), though his explanation of the make-up of the doubled chromosomes now seems doubtful. He noted also the occurrence of a tetraploid connective tissue cell, an abnormal condition commonly (if not constantly) present in the cells which form the sheath of the hemipteran testis and its smaller subdivisions. Hartman ('13) has more recently reported several cases in the spermatogonia and primary spermatocytes of the grasshopper (*Schistocerca* and *Melanoplus*) in which extraordinary chromosome numbers were encountered. Morgan ('15) has reported a case in *Phyllaphis* which differs from the above in that a considerable number of cells are affected rather than a few

isolated ones. In this particular instance all the cells of an entire cyst (male) contained the double number of chromosomes, which were readily counted, as the cells were just concluding the first spermatocyte division. This case presents one important point of difference from all other examples of abnormal division in that "the chromosomes are only half as large as are those at the corresponding stage of the normal spermatocyte stage"—a very unusual abnormality indeed.

In the material which I have examined two instances of abnormal chromosome number have been found which resemble the one described by Morgan in that large numbers of cells are affected, *but* the chromosomes are *not* reduced in size. A description of these cases will now be given.

The first, and in some ways the less interesting, of these cases was found in a specimen of *Loxa florida* Van D. (Family *Pentatomidæ*), of which both testes were affected in exactly the same way and to the same extent. This particular abnormality was restricted to a single lobe of the testis which happens to be composed of cells of an unusually small size (see Bowen '22).<sup>1</sup> The earlier stages in the affected lobe seem to be normal in every way (Fig. 4), but with the inauguration of the growth period of the primary spermatocytes a very unusual phenomenon sets in. Large numbers (but not all) of the cells in each cyst fuse together in pairs to form giant, bi-nucleate cells (Fig. 5). The cytoplasmic masses of the two cells seem to fuse completely, but the nuclei remain separate although they frequently become so closely appressed as to show little visible separation. As the growth period proceeds, this process of fusion goes on progressively, though somewhat irregularly, with the result that eventually the prophase cysts contain a heterogeneous mass of cells possessing in individual cases anywhere from one to eight or more nuclei (Fig. 6), each with its own complement of chromosomes.<sup>2</sup> The cells round out and become somewhat separated from each other, those containing numerous nuclei being roughly spherical in shape and of

<sup>1</sup> I have been able to examine only a single specimen of this species. It would be interesting to find out whether this abnormality has any relation to the sizes of the cells which might possibly cause its production repeatedly.

<sup>2</sup> In *Loxa* the spindle of the first spermatocyte division normally has eight chromosomes, as in a number of other pentatomids (*e.g.*, *Euschistus*).

extraordinary size. The nuclei themselves become more or less lobulated during the growth period and so are difficult to separate and count, but the grouping of the late prophase chromosomes shows that each nucleus retains its identity and that the fusion process involves only the cytoplasm of the uniting cells. The remarkable fact about these giant cells is that they seem to possess only the single set of centrioles characteristic of a normal cell. Often these are not diametrically opposite each other (as is customary in Hemiptera), and as the spindle is formed for the first maturation division it tends to develop toward one side of the cell, becoming later on symmetrically located. How the centrioles of each of the cells represented in one of these giant spermatocytes are reduced to a normal number is not known; possibly the loss occurs before the fusion, which might itself be dependent on such an abnormal condition. Further, the centrioles which do take part in the formation of the spindle, are not unusually large, as one might anticipate, but are in fact no larger than the normal ones, at least not conspicuously so. Spindles are normally developed, and the metaphase chromosome plates are formed in a characteristic manner (though slightly irregular in cells with large numbers of chromosomes). I have been able to count cases with 16 and about 32 chromosomes, the higher numbers being less satisfactory for counting. I have, however, counted considerably more than 60 chromosomes in a single plate. Second maturation spindles seem to be normally formed (except, of course, with respect to chromosome number) and spermatids of a variety of sizes result, each spermatid being formed on a large scale but in an otherwise normal fashion. Whether the giant sperms resulting from the multinucleate spermatocytes reach maturity was not definitely ascertained, but at least some of them seemed to be undergoing the earlier stages of normal differentiation.

The origin of this abnormality is obscure. However, the apparent fusion (?) of cells to form multinucleate masses is not altogether unknown, as such aggregates have been noticed by Wodsedalek<sup>1</sup> in a number of mammals, particularly the ground

<sup>1</sup> Only a very brief abstract of this author's results has been available; see Abstracts of Papers, American Society of Zoölogists, Nineteenth Annual Meeting, December, 1921.

squirrel (*Citellus*). In the last-mentioned case, the spermatids also are multinucleate, which would seem to preclude the possibility of their forming normal sperms—a point in which this case is quite different from the one described in *Loxa*.

The second instance of abnormal divisions falling under *Case 2* presents in many ways the most interesting features of all. It is clear that aside from the method just described of multiplying chromosome numbers by cell fusion, the same result might be produced by some failure in spermatogonial division, such that the daughter chromosomes would be incorporated in a single nucleus, while the extra set of centrioles in some way became suppressed or lost. Such might conceivably have been the genesis of the case described by Morgan ('15), and of various triploid and tetraploid 'mutations.' The case now to be described seems to belong in this category. It was found in a specimen of *Euschistus variolarius* P. B. (Family *Pentatomidæ*), which had been collected in the fall of 1918 by Professor Wilson (without of course, any suspicion that it was abnormal), and kept in the laboratory during the winter. Upon my return to Columbia in February, 1919, this bug, together with other specimens of *Euschistus*, was very kindly turned over to me by Professor Wilson. The abnormality was found in only one specimen (No. 94) (of those sectioned), and in only *one* testis of that specimen. The other testis was normal in respect to this particular irregularity, though both presented other abnormal features. Whether the stay in the laboratory under somewhat unfavorable conditions was in any way responsible for the abnormalities is by no means clear; but from the fundamental nature of the particular abnormality here to be considered, it would seem more probable that it arose during one of the earlier instars and was quite uninfluenced by the abnormal environment of the adult. The material happens to have been fixed in Benda's Flemming (with the omission of the mordanting customary in the Benda method itself), and stained in Fe-hematoxylin. This method, intended primarily for the demonstration of the mitochondria, is not entirely satisfactory for the study of chromatic features; but the preparations proved entirely adequate for the study of most of the necessary details.

This particular abnormality consists of a tetraploid chromosome

number in most of the cells of one of the large-celled lobes (lobe No. 4—Bowen, '22) of one testis. There are six lobes in the testis of *Euschistus* (Bowen, '22), and in this particular testis I have been able to make counts of spermatogonial metaphase chromosome plates in five of the lobes. In four of these (lobes No. 2, 3, 5 and 6—Bowen, '22) the number of chromosomes is 14 (normal for the genus (Montgomery, '11)), and it is clear from other evidence that the one lobe (No. 1) in which no spermatogonial divisions could be counted, is likewise normal in chromosome number. In one lobe (No. 4), however, the chromosomes are very clearly abnormal in number as could be readily told from numerous metaphase plates. The exact number was not easily arrived at because the plates tend to be a trifle irregular, but in one or two particularly good cases I have been able to count 28 chromosomes with satisfactory clearness (Fig. 7). In adjacent cysts of spermatogonia in which the nuclei are in early prophase stages it can also be easily seen that the chromosomes are present in abnormal number, though exact counts were of course impossible. In the growth stages of the spermatocytes and in the spermatid stages the double number of chromosomes can be surmised from the unusually large size of the cells, which increase is shared by the cytoplasm as well as the nucleus. The tetraploid condition is, therefore, present throughout the entire lobe, though not exclusively, for I was able to find an occasional cyst (growth period and spermatid) in which, judging from the comparative sizes of the cells, the chromosomes were present in the normal number. These facts lead me to suppose that an irregular division of a germ cell at some very early stage gave rise to an abnormal series of spermatogonial cells which formed the bulk of the cells in this particular lobe. Among these, however, were included a few normal cells which evidently gave rise to the normal cysts found scattered infrequently among the abnormal ones.

Analysis of the constitution of the metaphase spermatogonial plates with 28 chromosomes should bear out the view that the tetraploid chromosome number represents a simple doubling of the usual diploid group. Unfortunately, the chromosomes in *Euschistus* are not of strikingly different sizes, but in the case of the *Y* chromosome the difference is sufficiently marked to be read-



ily distinguished; and as examination of Fig. 7 will show, there are two *Y* chromosomes (the very small ones) instead of the usual one (compare Montgomery, '11, Fig. 2). It is, I think, fair to assume that the other chromosomes are similarly represented in a duplex manner, an assumption which accords with the view now generally accepted of the nature of tetraploid chromosome groups.

Synapsis is apparently accomplished in a normal manner, and after the "diplotene" threads have become spread throughout the nucleus it is possible, in favorable places, to see that the threads are arranged in *pairs* and not in *quartets* as one might conceivably expect. In other words the homologous chromosomes are paired off just as they would have been in the presence of the diploid chromosome number, except that in each tetraploid nucleus there are two similar pairs instead of one. During the so-called confused period, when the chromatin threads become indistinct, the sex chromosome nucleoli stand out with great clearness. We should expect in a tetraploid nucleus four such nucleoli (barring possible fusions such as sometimes normally occur), representing two *X* (larger) and two *Y* (smaller) chromosomes. This expectation is exactly realized (Fig. 8), another bit of evidence which tends to prove that we are dealing here with a case of true tetraploidy.

When the chromosome tetrads condense in the prophases of the first maturation division, they resemble in every way the tetrads of the normal spermatocytes. (Compare Fig. 9 with Montgomery ('11), Figs. 86, 88 and 93.) It is clear beyond question that homologous chromosomes have paired off in a perfectly normal manner. These tetrads become condensed in the usual way to form the definitive chromosomes of the first maturation division, and the spindle of this division, when seen in side view (Fig. 10), presents no unusual features (except of course for the chromosome number). There happened to be one cyst of cells in various phases of the first spermatocyte division and these dividing cells have been carefully studied. I have been able to find nothing in the manner of spindle formation or chromosome division in any way abnormal, except that the plates have the diploid rather than the haploid number of chromosomes. This

point was studied with special care. Two metaphase plates in polar view were found in which the chromosomes could be readily counted, although both were a trifle irregular in arrangement. One of these plates (Fig. 11) seemed to be in the final stage of formation, and some of the chromosomes were still not completely oriented. Fortunately this was particularly true of the *Y* chromosomes, whose constitution was thus rigorously demonstrated. In the normal cells the *Y* chromosome is represented by a dyad which is divided in the first spermatocyte division (see Montgomery, '11, Fig. 94). In a tetraploid cell we should expect to find two such dyads, and this is actually found to be the case. The *Y* chromosomes have not conjugated, but each has behaved exactly as though the other were absent. The parts of the dyad have been in each case precociously separated (Fig. 11). Furthermore, two unusually large chromosomes can be readily picked out (*A* and *A'*), and these seem to correspond to the single large chromosome of the normal haploid plate (see Wilson, '05*a*, Fig. 3*a*). A count of all the chromosomes (counting the *Y* dyads each as a single chromosome) gives a total of 17—one more than the expected number (16, or 8 times 2). It seems likely that the extra chromosome may be due to the counting of an *X* dyad, the parts of which have become separated, as two chromosomes instead of a single one. In Fig. 12 another plate is given which, judging from its neighbors, is probably in a very early anaphase stage. The plate is somewhat more compact, and the *Y* chromosomes, now presumably being drawn apart, are seen as single chromosomes. In this plate 16 chromosomes are clearly to be counted, although one of them is irregularly placed.

Unfortunately no second maturation divisions were found, so that it was impossible to check up the behavior of the *X* and *Y* chromosomes in that division. The spermatids seem to be normal in every way, except that they are larger than is usual; and at least the earlier stages of differentiation are gone through in a normal manner. Subsequently, some of them certainly become abnormal, but so do some of the sperm in an adjacent lobe (No. 6); and it is, therefore, impossible to tell whether the degeneration is connected with the tetraploid condition or not.

## CASE 3.

The occurrence of divisions with abnormal numbers of both chromosomes and centrioles is of common occurrence in the maturation divisions in Hemiptera (see for example Henking, '91), and such divisions have also been described in spermatogonia (Montgomery, '98), and in cells from the connective tissue of the testis (Paulmier, '99). The general features of these divisions are well known, and they probably originate from abnormal spermatogonial divisions in which the daughter chromosome groups have failed to produce separate nuclei. In the cases here noted, from *Chlorochroa uhleri* (= *persimilis*) Stål (Family *Pentatomidæ*), large numbers of cells were affected particularly along one half of one testicular lobe, and to a lesser degree the contiguous portion of an adjacent lobe. In some cysts, as could be told from the unusual size of the nuclei with extra chromosomes, large numbers of spermatocytes (and spermatids) were affected, while in others all the cells were normal. The causative agent operative in this case would accordingly seem to differ from the more or less accidental sources of abnormal division figures. The chief interest of this case lies in the fact that the material had been prepared to demonstrate the Golgi apparatus, and it was accordingly possible to study the distribution of the dictyosomes (fragments of the Golgi apparatus) in relation to the multipolar spindle.

Numerous cases of tripolar<sup>1</sup> spindles in the first maturation division were found at both the metaphase (Fig. 2) and late anaphase (Fig. 1) stages, of which two are figured. As I have shown in another place (Bowen, '20), the dictyosomes collect (in equal amounts) around the ends of the normal (bipolar) spindle at the beginning of the metaphase, a position which they maintain during the anaphase, the Golgi material being thus distributed with approximate equality to the daughter cells. I suggested that the centrioles represent the morphological foci of the influences which bring about this equal distribution of the Golgi material.

<sup>1</sup> There were also numerous cases in which the centriole number was normal, but with abnormal chromosome numbers, as in Case 2; but as these presented no points of special interest, they are not here considered. The distribution of the dictyosomes was in accordance with the expectation for a bipolar spindle.

If this suggestion be correct, in tripolar spindles the dictyosomes should obviously be arranged around each spindle pole (centriole) in a manner similar to that found in bipolar figures. This, is, in fact, the case as the figures show very clearly (Figs. 1 and 2), and seems to contribute additional evidence to that already accumulated tending to demonstrate an element of unusual regularity in the distribution of the Golgi apparatus in cell division.

#### DISCUSSION.

Abnormal mitoses in the male germ cell cycle are chiefly of interest from the standpoint of the sperms which might be produced as a result of such divisions. It is clear that the sperms derived from divisions belonging to *Case 1* would always be abnormal; and those of *Case 3* (if the division were ever completed, which seems doubtful<sup>1</sup>) would likewise be abnormal in the great majority of cases. Whether any such abnormal sperms ever take part in successful fertilization is questionable. After divisions of the *Case 2* variety, however, there is no reason for supposing that the resultant sperms might not behave in an entirely normal manner in fertilization. This is particularly true of the case which I have described in *Euschistus*, and to the possibilities there presented I should like to give particular attention.

It is evident that tetraploid spermatogonia would probably give rise to diploid primary spermatocytes, and this probability has been definitely proved in the *Euschistus* case. It seems equally probable that the resultant sperms would likewise contain a group of chromosomes in the diploid rather than the normal, haploid number. Unfortunately definite proof of this has not been obtainable, but everything indicates that such is actually the case. If such diploid sperms should fertilize a normal (haploid) egg, a triploid individual would result; and if, as an almost impossibly rare coincidence, the egg should also be diploid, through some abnormality, a tetraploid individual would result. The triploid individuals might be numerous due to the involvement of a large number of sperms, but they would be accompanied by diploid individuals derived through some of the normal, haploid sperms

<sup>1</sup> It is perhaps more probable that these abnormal mitoses fail, giving rise to the familiar giant spermatids with one large nucleus but a multiple set of centrioles.

which are produced by the normal portions of the testis. It is interesting to note that Bridges ('21) has recently reported a case of triploidy in *Drosophila* which exactly fulfills these expectations. The egg rather than the sperm, as could be determined from genetic evidence, happens, however, to have been the gamete affected, but the arrangement of the ovary is such that the difference in sex does not affect the applicability of the argument. The facts which I have been able to make out in *Euschistus* prove (so far as they go) that the presence of the chromosomes in the tetraploid number, following some irregularity of unknown origin, in no way affects the normal progress of spermatogenesis<sup>1</sup> (and presumably of oögenesis as well). This is, I believe, the first cytological evidence that abnormal germ cells, once established, may thereafter proceed in an entirely normal manner—probably with the ultimate production of functional sperms (or eggs).

These facts have a very interesting bearing on the origin of triploid and tetraploid individuals, a matter in regard to which opinion is at present in a very unsettled state. It has been held by Gates ('09), with the subsequent assent of Strasburger, that the doubling of the chromosome number (tetraploid individuals) might arise "as the result of a suspended mitosis in the fertilized egg or in an early division of the young embryo." Stomps ('12), on the other hand, has suggested that tetraploid individuals may result from the union of two diploid gametes, triploid individuals being obviously formed on this hypothesis by the union of a haploid with a diploid gamete.<sup>2</sup> Further, the nature of the chromosome group in a diploid gamete is again open to a difference of opinion, since it is evident that the diploid number may have arisen from a normal (diploid) auxocyte through failure of

<sup>1</sup> Provided of course that other disturbing elements such as multiple centrioles are absent.

<sup>2</sup> The possibilities of polyspermy have also been considered by Gates particularly in cases of triploidy, but our knowledge of this condition in animals lends no support to the belief that it is ever a factor in the production of triploid or tetraploid individuals. Further, both these authors were interested almost exclusively in plants (in which (*Ænothera*, for example) triploid and tetraploid individuals have actually arisen under observation), in which further special possibilities (apogamy, for example) have to be considered that are not met with in animals. These matters need not be considered further in this paper.

reduction, or from a tetraploid auxocyte after normal reduction has occurred.

My observations indicate that the requisite conditions for the origin of the triploid, and perhaps tetraploid, individuals may be fulfilled by a combination of the possibilities suggested by the hypotheses outlined above. Thus, it seems certain in the *Euschistus* case that a suspended (or otherwise abnormal<sup>1</sup>) mitosis has occurred during some early division in the germ cells, giving rise to a tetraploid condition confined to the descendants of the particular cell involved. If, as seems probable, each cyst of spermatogonia is derived by the repeated division of a *single* cell derived from an early germ cell, the occurrence of the tetraploid cysts would be accounted for, and also the diploid cysts produced concurrently from the early germ cells of normal constitution. The spermatocytes descended from the tetraploid cells have undergone a *reduction* in the proper sense of the term, but the *number* of chromosomes in the resultant gametes is undiminished ("unreduced") as compared with the number in the normal (haploid) ones. The fusion of such a diploid gamete with a normal one would obviously produce a triploid individual. An explanation along these lines seems to me preferable to the one sometimes given which explains triploidy as due to the union of a normal and an unreduced (properly speaking) gamete; for while such unreduced gametes have been supposed to arise (in Hemiptera) through the suppression of one (or both) of the maturation divisions, they always contain an abnormal number of centrioles (as Paulmier, '99, long ago showed), and the weight of evidence is against the probability of their functioning normally in fertilization.

The origin of tetraploid individuals by this method would depend upon an exceedingly rare coincidence, and, as a matter of fact, tetraploidy in animals seems to be a rather rare phenomenon.

<sup>1</sup> The case of *Loxa* suggests the possibility that a tetraploid germ cell might arise from the fusion of two normal ones. By analogy such a fusion product might well contain the normal centriole content, as observed in *Euschistus*. The usual explanations advanced to account for the doubling of chromosomes all fail to account for the observed normal number of centrioles—an important part of the story, which has not yet received adequate attention. In this connection it is of interest to note that centrioles are generally absent in the higher plants.

In plants, on the other hand, it occurs more commonly—in *Oenothera* for example, where the repeated occurrence of unusual chromosome complexes would perhaps indicate that some unstable condition exists which would increase the probability of a coincident production of diploid gametes of both sexes.

The viewpoint which I have here tried to develop may be summarized in the following way. A normal, diploid zygote is formed by the union of two haploid gametes.<sup>1</sup> After a number of divisions the germ cells (one or more?) are segregated, and these then multiply to form the primordial germ cells and subsequently spermatogonia (or oögonia). An abnormal division at some early stage resulting in a doubling of the chromosomes might conceivably give rise to a gonad composed entirely of tetraploid cells—a condition never yet observed. A similar abnormal division in one of the primordial germ cells would result in many cysts of tetraploid spermatogonia (or oögonia), as I have found in the *Euschistus* case—certainly a rare phenomenon or it would have been long since reported. Proceeding still further, a similar abnormal division at the time a cyst of spermatogonia (or oögonia) is begun, would give rise to a single cyst of tetraploid cells (see the case reported by Morgan, '15), while abnormal divisions at a subsequent time might give rise to one or several tetraploid cells among many normal ones in the same cyst. The tetraploid cells thus produced undergo normal *synapsis* and *reduction*, but the chromosome number, being thus diminished only by the usual one half, is diploid in the resulting gametes. The union of such a diploid gamete with a normal (haploid) one produces a triploid individual, while the union of two such diploid gametes (due to a very rare coincidence) produces a tetraploid individual.

In conclusion, it may be noted that the behavior of the chromosomes in the *Euschistus* case adds further evidence to that already accumulated tending to demonstrate the genetic continuity of the chromosomes. In the same testis there are (normal) diploid and (abnormal) tetraploid spermatogonia, each of which gives

<sup>1</sup> It is conceivable that, as Gates suggests, the first (or other early) cleavage might be suppressed, resulting in a tetraploid individual, but there is no evidence among animals that this ever occurs, and the difficulties in the way of such an explanation are great.

rise to the expected haploid and diploid chromosome complexes in the maturation divisions. The fact that in synapsis (and subsequent stages) the homologous pairs of chromosomes behave exactly as though they were present in the diploid number, is another fact of great theoretical significance. This last-mentioned point is of particular interest because of the condition recently reported in a triploid specimen of *Canna* by Belling ('21). This author finds that in the pollen-mother-cells there are nine *triads* (the haploid number is nine), "each of which separates into two and one on the spindle, in a random manner with regard to the two poles." In the tetraploid individual of *Euschistus*, on the other hand, no indication of a tendency to form multiple groupings of this kind has been observed at any stage.

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## EXPLANATION OF PLATES.

All of the figures have been outlined as far as possible with the camera lucida at an initial enlargement of approximately 3,800 diameters. The outlines have been extensively corrected and details added free hand. In reproducing, the figures have been reduced uniformly to an enlargement of approximately 3,000 diameters. In every case the method employed in the preparation of the original object has been indicated.

*P*, plasmosome; *X* and *Y*, idiochromosomes.

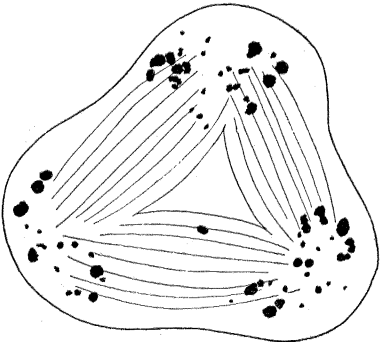
## PLATE I.

FIGS. 1 and 2 are from *Chlorochroa uhleri*; Fig. 3 is from *Chelinidea vittiger*; Figs. 4, 5 and 6 are from *Loxa florida*. With the exception of 1 and 2, the original preparations were from material fixed in Flemming and stained with Fe-hematoxylin.

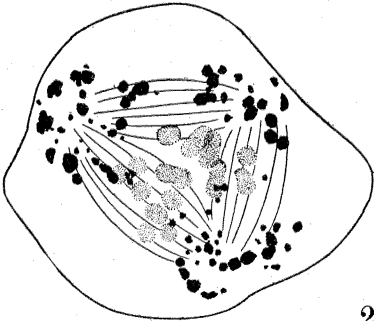
FIGS. 1 and 2. Tripolar spindles in the first spermatocyte division. Some of the chromosomes (stippled) are indicated in Fig. 2. (Osmic impregnation.)

FIG. 3. Tripolar spindle with normal number of chromosomes in the first spermatocyte division.

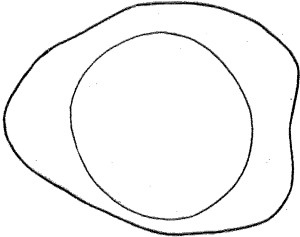
FIGS. 4, 5 and 6. Primary spermatocytes in the later diplotene stage and in the earlier and later growth period, showing progressive fusion of the cytosomes.



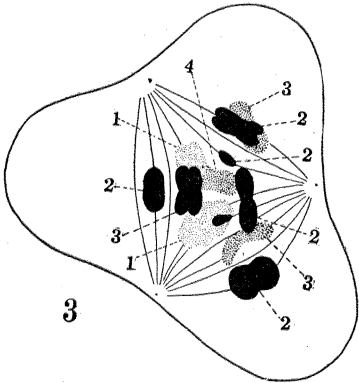
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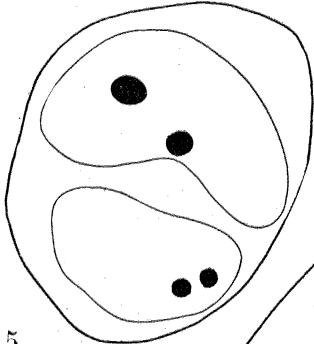
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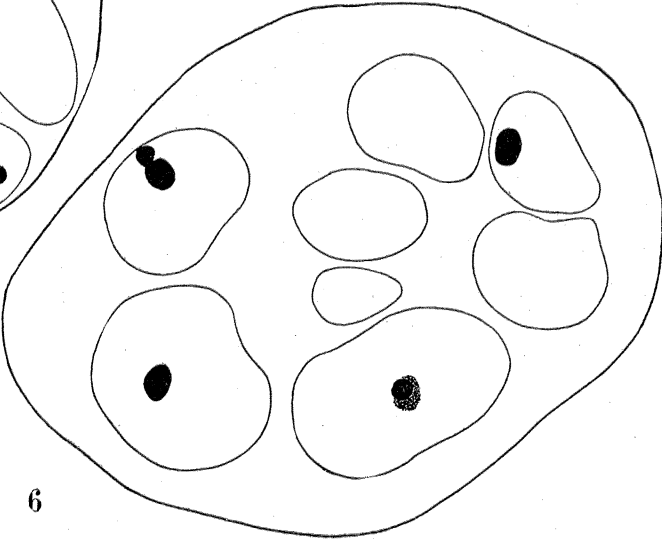
4



3



5



6

## PLATE II.

All the figures are from *Euschistus variolarius*. The original preparation was from material fixed in Benda's Flemming and stained with Fe-hematoxylin.

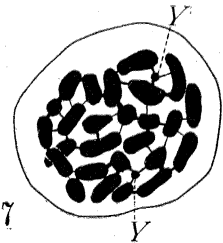
FIG. 7. Spermatogonial division (polar view) showing metaphase plate with 28 chromosomes.

FIG. 8. Primary spermatocyte in the later growth period.

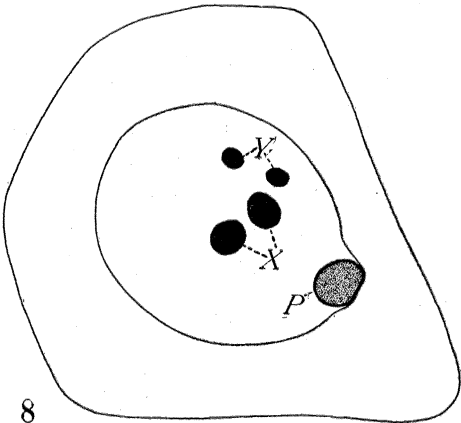
FIG. 9. Single tetrad from a tetraploid spermatocyte nucleus in the late prophase.

FIG. 10. First spermatocyte division; lateral view.

FIGS. 11 and 12. Early and late stages in the metaphase (approximately) of the first spermatocyte division; polar view.



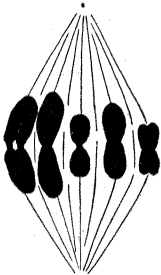
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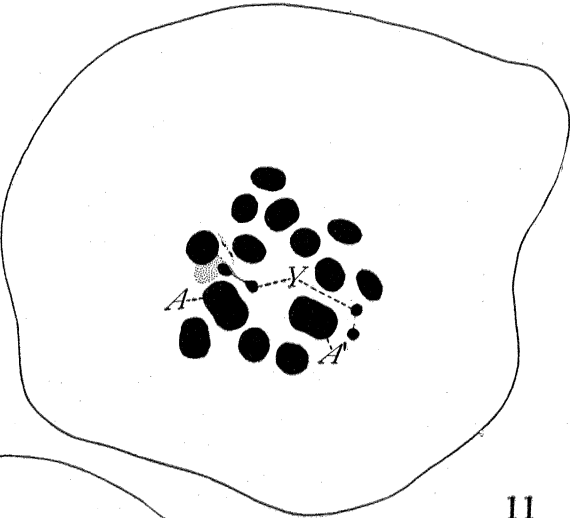
8



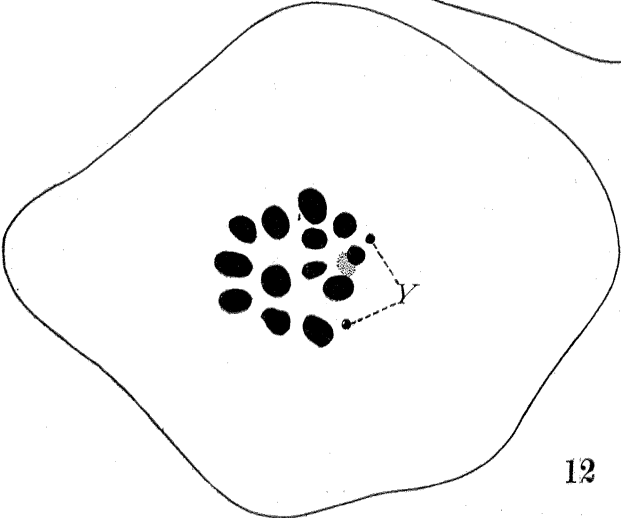
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10



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